ELSEVIER

Estimating *Arundo donax* ramet recruitment using degree-day based equations

David F. Spencer *, Gregory G. Ksander

USDA-ARS Exotic & Invasive Weeds Research Unit, Robbins Hall, 1 Shields Avenue, Davis, CA 95616, United States

Abstract

Arundo donax is a tall perennial reed. Once established, it spreads by producing new shoots (ramets) from rhizomes. We performed two separate experiments to test the hypotheses that temperature (7, 8, 14, 16, or 20 °C) and combinations of temperature and nitrate concentration (0, 0.3, 0.6,1.2, 2.4, 3.6, 4.8, and 6.0 mg/l nitrate) regulated the initiation of ramet production. No ramets emerged from rhizome sections at 7 or 8 °C, but ramets emerged at 14, 16, and 20 °C. Neither time to ramet emergence nor the number of ramets that emerged was influenced by nitrate level in the watering solution. We used the above results in combination with ramet emergence data from plants grown outdoors at Davis, California to develop degree-day equations for three separate ramet cohorts. When compared to ramet emergence from different plants in different years, there was very good agreement between predicted and actual ramet emergence indicating that these equations provide a realistic representation of processes involved in ramet emergence. This is an important step in developing integrated management plans for this species.
Published by Elsevier B.V.

Keywords: Phenology; Giant reed; Rhizome; Sprouting

1. Introduction

Invasive plant species significantly alter ecosystem structure and function (Vitousek, 1990; Vitousek et al., 1997). *Arundo donax* is an invasive weed in California riparian zones (Bell, 1997). It is a tall perennial reed frequently found growing in water and is classified as an emergent aquatic plant (Cook, 1990). It is morphologically similar to *Phragmites australis,* except that it is much larger and more robust in appearance (DiTomaso and Healy, 2003). It occurs in large dense clumps up to several meters across and containing stems (up to several hundred per clump) that may reach 8 m in height (DiTomaso and Healy, 2003). Although *A. donax* produces flowers, no viable seeds have been detected for plants growing in California (DiTomaso and Healy, 2003). Thus, once established, it spreads by clonal expansion, which is dependent on the production of new ramets from rhizomes. Lewandowski et al. (2003) reported that shoots are produced during the whole growing season from large rhizomes. In California, spring and summer are the main growing season for new ramets (Decruyenaere and Holt, 2001;

Wijte et al., 2005). However, little is known about the specific environmental cues that regulate initiation of ramet production in spring. Predicting ramet emergence will be central to developing integrated management approaches (Wilen et al., 1996) and may enhance overall understanding of plant phenological patterns (Rathcke and Lacey, 1985).

Predictions of plant growth have been successfully based on the accumulation of heat units or degree-days (Fitter and Hay, 2002; Thornley and Johnson, 1990). Degree-day based equations have been helpful in forecasting the initiation of growth from vegetative propagules or seeds. Spencer and Ksander (2001) and Spencer et al. (2000) demonstrated that sprouting and emergence from vegetative propagules of several species of weedy aquatic plants (*Hydrilla verticillata*, *Potamogeton pectinatus*, *P. nodosus*, *Vallisneria americana*) could be predicted with equations based on accumulated degree-days. Wilen et al. (1996) reported that sprouting of yellow nutsedge (*Cyperus esculentus*) could be accurately predicted using degree-day models.

We performed two experiments and monitored ramet emergence and temperature in two additional outdoor studies during 1999, 2000, 2001, and 2002. These experiments tested the hypotheses that *A. donax* ramet emergence (1) was influenced by temperature, (2) could be predicted from

* Corresponding author. Tel.: +1 530 752 1096; fax: +1 530 752 4604.
  E-mail address: dfspencer@ucdavis.edu (D.F. Spencer).

accumulated degree-days, and (3) was stimulated by the levels of nitrate in the soil solution, as has been reported for seed germination (Karssen and Hilhorst, 1992).

2. Methods

2.1. Rhizome sprouting versus temperature

In the first experiment, *A. donax* rhizome sections (3.5 cm long, see Boose and Holt, 1999) and stem cuttings (3.5 cm long including a node), collected from large mature plants growing near Putah Creek, California in February, 1999, were planted individually in pots containing modified UC Mix (Spencer and Anderson, 1986). There were eight pots containing rhizome sections and eight pots containing stem cuttings at each temperature. They were placed in growth chambers and maintained at 7, 14, or 20 °C in the dark. At 2- to 3-day intervals they were checked for sprouting and the date was recorded when the stem/rhizome piece in a particular pot sprouted. After 12 weeks, plants were harvested and the dry weights of all new growth and of the original rhizome piece were determined after drying at 80 °C (Coombs et al., 1985).

2.2. Rhizome sprouting versus temperature and nitrate

Previous research with seeds indicated that nitrate and temperature might interact to influence germination (Karssen and Hilhorst, 1992). We hypothesized that *A. donax* rhizome sprouting would be affected by temperature and nitrate concentration. In this factorial experiment, treatment units consisted of a 3.5-cm segment of *A. donax* rhizome in a plastic plot filled only with clean sand. The sections were originally collected from large mature plants growing at near Cache Creek, California in January, 2000 and cut into 3.5 cm segments that included one node. There were 10 pots for each treatment. The nitrate treatment consisted of weekly watering of the pots with 100 ml of one of the following solutions made with deionized water: 0, 0.3, 0.6, 1.2, 2.4, 3.6, 4.8, and 6.0 mg NO_3/ liter for 14 weeks. One set of 80 pots was placed in each of two growth chambers with temperatures set at either 8 or 16 °C. Pots were maintained in darkness, except for brief periods when sprouting was checked. At 2–3-day intervals we examined the pots and recorded the date of sprouting.

2.3. Outdoor studies

We conducted two outdoor studies. In the first, two 3.5-cm rhizome sections of *A. donax* were planted outdoors on February 12, 1999 at the Exotic & Invasive Weeds Research Unit, Davis, California. The rhizome sections, collected from a site adjacent to Putah Creek, were planted in a 45.5 cm diameter PVC pipe that was 91.5 cm tall with 60 cm of modified UC Mix. During the spring and summer, plants were watered at two to three day intervals. Ramet emergence was monitored at 2–3-day intervals until November, 2000.

A second set of six plants was started on May 12, 2000 by planting six of the sprouted rhizome sections from the temperature/nitrate study in individual large fiberglass tanks (one rhizome section per tank, tank dimensions were 30 cm deep × 116 cm wide × 189 cm long) filled with topsoil. At planting, ramet lengths were 14, 13.1, 9.5, 12.5, 6.5, and 8 cm. In both studies, soil temperature was monitored at hourly intervals using data loggers (Wescor Inc., Logan, UT; Onset Computer Corp, Bourne, MA).

Using the soil temperature data, we calculated degree-days with the single triangle method using equations (Table 1) described by Zalom et al. (1983). We estimated the lower threshold (7 °C) for sprouting from the results of the two experiments. We chose 30 °C as the upper threshold based on the discussion of temperature influences on the growth of perennial grasses in Gates (1980) and the report by Rossa et al. (1998) indicating that *A. donax* photosynthesis was reduced at temperatures >30 °C. When calculating accumulated degree-days, it is necessary to determine the starting point, i.e. the date to begin accumulating degree-days. An examination of the temperature data for 1999 and 2000 indicated that low temperatures occurred around the end of December to the beginning of January. Since these temperatures were less than the temperature thresholds, we started accumulating degree-days beginning January 1.

2.4. Statistical analysis

In the first growth chamber experiment we calculated an analysis of variance to test for significant effects of temperature on the dry weight of new ramets produced. We also performed logistic regression to test for associations between temperature and the proportion of rhizome sections or stem pieces that

Table 1
Equations used to calculate degree-days by the single triangle method of Zalom et al., 1983

Conditions[a]	Equation
If mxtemp > tup and mntemp > tup	Degree-days = tup − low
If mxtemp < low and mntemp < low	Degree-days = 0
If mxtemp < tup and mntemp > low	Degree-days = (6 (mxtemp + mntemp − (2low)))/12
If mxtemp < tup and mntemp < low	Degree-days = ((6 (mxtemp − low)^2)/(mxtemp − mntemp))/12
If mxtemp > tup and mntemp > low	Degree-days = ((6 (mxtemp + mntemp − (2low)))/12) − ((6(mxtemp − tup)^2)/(mxtemp − mntemp))/12)
If mxtemp > tup and mntemp < low	Degree-days = (((6 (mxtemp − low)^2)/(mxtemp − mntemp)) − ((6(mxtemp − tup)^2)/(mxtemp − temp)))/12

[a] Mxtemp, maximum daily temperature; mntemp, minimum daily temperature; tup, upper temperature threshold; low, lower temperature threshold.

sprouted. In the second growth chamber experiment, we performed event-time or failure-time analysis (Cantor, 2003) to test for associations between either temperature or nitrogen and the time to sprouting. Logistic regression was not appropriate for these data due to complete data separation (i.e., lack of sprouting at one temperature treatment) that occurred in this experiment. These calculations were performed with SAS software (SAS Institute Inc., 1999).

Using the number of ramets that emerged during 2000 (i.e., during the second growing season) in the first outdoor experiment, we calculated the proportion that had emerged on each sampling date by dividing the number present on that date by the total number that emerged by the end of the growing season. Resulting proportions were analyzed by logistic regression (SAS Institute Inc., 1999). We chose to use the logistic function, also known as the autocatalytic function, because it has been widely used to describe plant growth data, it often yields very good fits to empirical plant growth data, and it is especially appropriate for binary data (Hunt, 1982; Allison, 1999; Goudriaan and Van Laar, 1994). We fit the following equation for the 2000 sprouting data from the first outdoor study with accumulated degree-days as the independent variable:

$$\text{Proportion sprouted} = \frac{e^{\text{logit}}}{1 + e^{\text{logit}}},$$

where   logit = intercept + (coefficient × ACH   (accumulated degree-days)).

We also used the PROBIT procedure in SAS to calculate inverse predictions, to obtain the accumulated degree-days associated with various levels of ramet emergence.

To assess the predictive capabilities of the model, the model estimated number of stems (MENS) was compared to the actual number of stems (ANS) by linear regression where MENS was used as the predictor variable (X) and ANS was used as the independent variable (Y). If the model provided good estimates of the actual values then such a regression should yield equations with y-intercepts of 0 and slopes of 1 (that is, $Y = X$), indicating a direct correspondence between the estimated and measured values. In addition to the t-test performed within the regression procedure for testing the hypothesis that each parameter was different from 0, we performed a t-test to determine if the slope was significantly different from 1. We did this by dividing the difference between one and the slope by the standard error of the slope (Sokal and Rohlf, 1995). The resulting value was compared with a t-value associated with $\alpha = 0.025$ and infinite degrees of freedom. If the slope was not significantly different from 1, and the intercept was not significantly different from 0, then the model predictions match directly with the actual values.

3. Results and discussion

3.1. Growth chamber studies

In the first experiment, new ramets emerged and survived at 14 and 20 °C (Fig. 1). No ramets emerged from rhizome
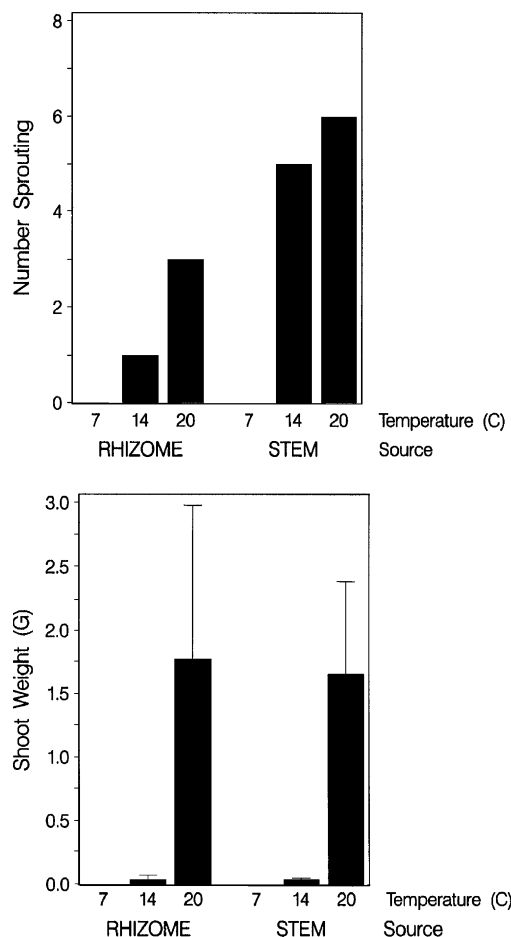

Fig. 1. Influence of temperature on *Arundo donax* ramet emergence (upper) and ramet weight (lower) after 12 weeks at constant temperature. In the upper graph values plotted are the number of rhizomes that produced ramets out of 10 replicates at each temperature and in the lower graph values plotted are the mean and 95% confidence limits for individual plant weights.
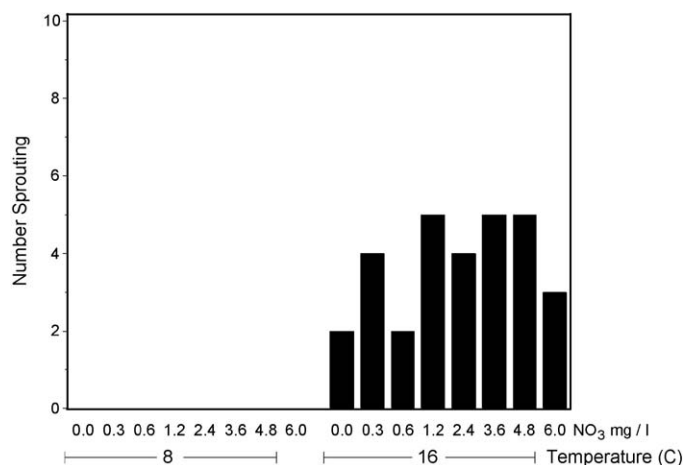

Fig. 2. Influence of temperature and nitrate on *Arundo donax* ramet emergence after 14 weeks at constant temperature. Values plotted are the total number of rhizomes that produced ramets out of 10 replicates at each treatment combination.

sections at 7 °C. A single ramet emerged from a stem cutting at 7 °C but died shortly thereafter. The proportion of ramets that emerged was significantly associated with temperature (Wald Chi-Square = 7.15, $P = 0.0075$) but not with the initial propagule type (stem versus rhizome) (Wald Chi-Square = 3.21, $P = 0.073$). Temperature significantly influenced the weight of newly produced ramets ($F_{2,42} = 5.28$, $P = 0.009$) but propagule type did not ($F_{2,42} = 0.01$, $P = 0.93$). The interaction term was not significant ($F_{2,42} = 0.01$, $P = 0.99$). In the second experiment, new ramets emerged at 16 °C, but not 8 °C (Fig. 2). Event-time analysis indicated that time to ramet emergence was not influenced by nitrate level in the watering solution (Chi-Square = 0.41, $P = 0.52$).

The results from these experiments indicated that contrary to information from seed germination trials (Karssen and Hilhorst, 1992), *A. donax* ramet emergence was not initiated in response to increased nitrate levels in the soil solution. Ramet emergence was influenced by temperature. In constant temperature growth chamber studies the lower threshold for ramet emergence was between 8 and 14 °C, while data from plants grown outdoors and exposed to fluctuating temperatures suggested that the lower threshold was 6.9 °C (see below). Results of these different studies are similar given the differences in culture conditions.
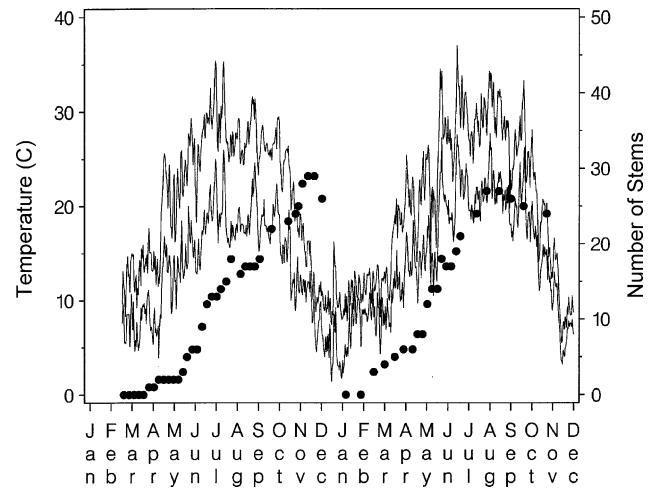

Fig. 3. Minimum and maximum daily soil temperatures (line) and number of *Arundo donax* ramets (dot) during 1999 and 2000 at Davis, California.

3.2. Outdoor studies

Minimum and maximum daily soil temperatures fluctuated within any given week, but displayed typical seasonal increases for both 1999 and 2000 (Fig. 3). During 2000, ramets first
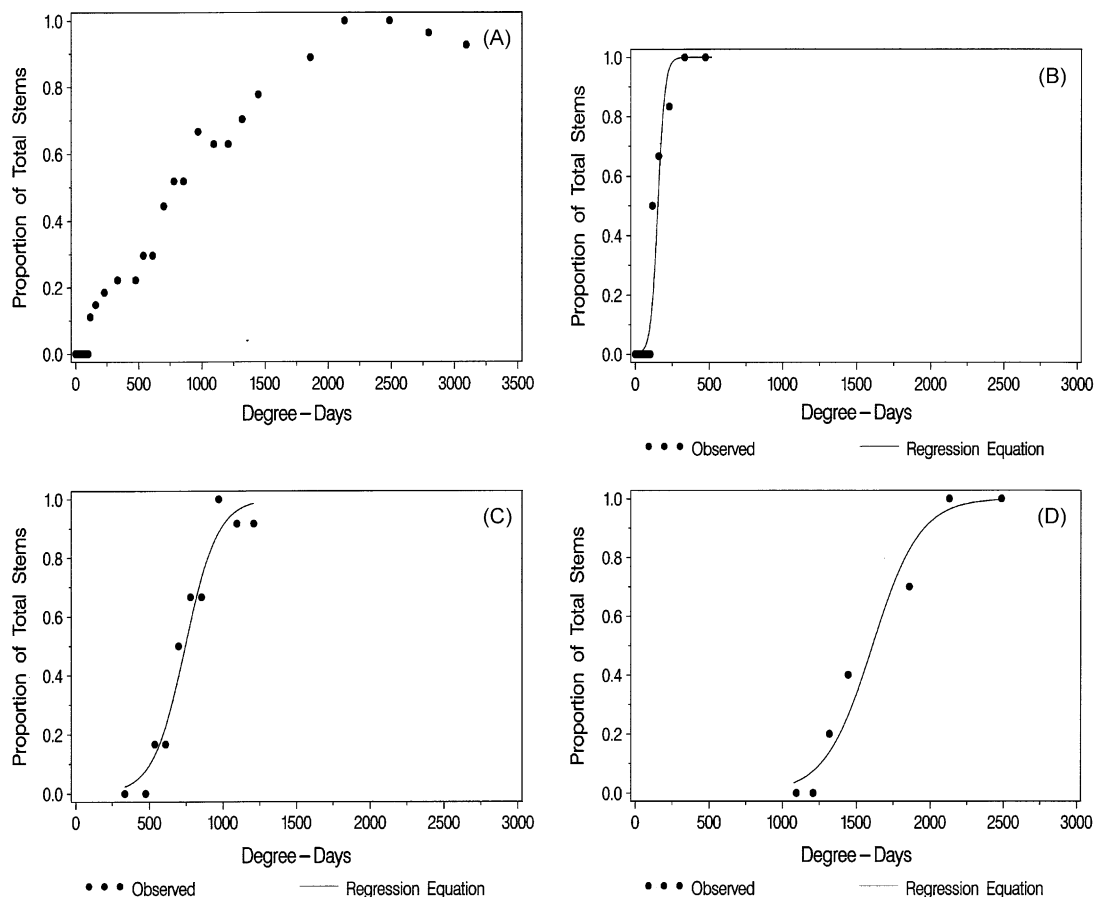

Fig. 4. Relationships between the number of *Arundo donax* ramets and accumulated degree-days for an individual plant during 2000 at Davis, California (A). Comparisons of the equations (solid line) fit by logistic regression and observed values for cohort 1 (B), cohort 2 (C), and cohort 3 (D) from the 2000 data set.
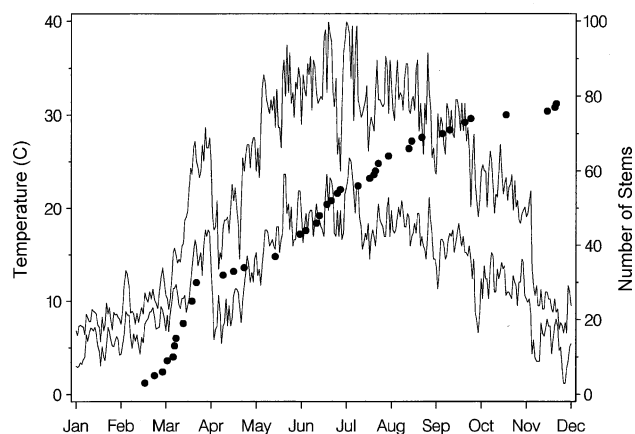
Fig. 5. Minimum and maximum daily soil temperatures (line) and combined number of *Arundo donax* ramets (dot) for six individual plants in six separate containers during 2001 at Davis, California.

emerged around March 26 when the average temperature of the preceding week was 11.8 °C. New ramets continued to emerge until November 4 when the mean temperature for the preceding week was 15.6 °C (Fig. 3). A total of 29 ramets were produced in 1999. In contrast, during 2000, ramet emergence began around February 15 when the average temperature for the preceding week was 10.6 °C and continued through early December when the weekly temperature was 5.2 °C. The observations for 2000 are likely more representative of undisturbed conditions since it represents ramet emergence from rhizomes, which had been planted at the beginning of the prior growing season. During 2000, 26 ramets emerged. Similar to the report by Decruyenaere and Holt (2001) for plants grown in southern California, most ramets emerged in May, June, and July for both 1999 and 2000.

For the 2001 outdoor study, minimum and maximum daily soil temperatures fluctuations were similar to those observed for 1999 and 2000 (Fig. 4). However, soil temperature increased earlier during 2001 than during the previous 2 years. Ramet emergence from rhizomes that had been established during 2000 was first observed in mid-February, 2001 when mean soil

temperature of the preceding week was 6.9 °C. Between 15 and 24 new ramets per plant emerged during 2001. Ramet emergence in 2001 displayed a more rapid early season increase than was observed in 2000 (Fig. 4).

Fig. 5 shows the relationship between ramet emergence and accumulated degree-days for 2000. Initial attempts to develop a single equation for this data set proved unsuccessful (based on results of goodness of fit tests). Upon closer examination of the pattern of ramet emergence and accumulated degree-days for 2000, it became apparent that at least three cohorts of ramets could be identified (Fig. 5). The first cohort had emerged by the accumulation of 525 degree-days. The second set of ramets began to emerge later and was complete by the accumulation of 1210 degree-days. Emergence of the third cohort was finished by the accumulation of 2500 degree-days. The production of discrete cohorts of ramets has not been reported before for this species and a mechanistic understanding of the processes involved is not known for certain. However, information from studies with other grass species shows distinct ramet hierarchies, and several mechanisms have been proposed for regulating ramet production by grasses including, apical dominance, intra- and interclonal competition for resources, physiological integration, and the red:far-red radiation ratio within a clone (Briske and Derner, 1998).

A logistic regression equation relating proportion of ramets emerged to accumulated degree-days was derived for each cohort (Table 2). We calculated the number of degree-days required to achieve a given proportion of ramet emergence for each cohort (Table 3), which has direct application in evaluating the timing of various control techniques.

As a further test of the predictive capabilities of these equations, we used minimum and maximum daily temperatures from the 2001 and 2002 data sets to predict ramet emergence for 2001 and 2002. (These data are from the second and third years of this experiment.) These predictions compare favorably to the actual data for 2001 and 2002 (Fig. 6). There is good agreement in both the timing and magnitude of predicted ramet emergence for both years and the observed ramet emergence for both years, indicating that these equations provide a realistic

Table 2

Analysis of maximum likelihood estimates for logistic regression of proportion of ramets emerged versus accumulated degree-days (ACH) for three cohorts of *Arundo donax* ramets

Variable	d.f.	Parameter estimate	Standard error	Wald Chi-Square	$Pr >$ Chi-Square	Sommer's D
Cohort 1–ACH < 525						
Intercept	1	−6.4284	1.4036	20.9768	<0.0001	0.98
ACH	1	0.0420	0.0107	15.5667	<0.0001	
Cohort 2–ACH > 335 and <1210						
Intercept	1	−6.8064	1.1964	32.3673	<0.0001	0.82
ACH	1	0.00913	0.00159	32.9335	<0.0001	
Cohort 3–ACH > 1070 and <2500						
Intercept	1	−10.1220	2.1366	22.4434	<0.0001	0.90
ACH	1	0.00629	0.00138	20.6968	<0.0001	

Intercept and slope (multiplied by ACH) are used to estimate logit from the equation logit = intercept + slope × ACH (accumulated degree-days). The proportion of ramets emerged is then estimated using the equation, $P = e^{(logit)}/(1 + e^{(logit)})$. Wald Chi-square and its probability test the null hypothesis that the parameter does not differ from zero. Sommer's D is a measure of correlation between the predicted and observed data. It ranges from 0 to 1. For more information see Allison (1999).

Table 3
Predicted accumulated degree-days (ACH) required to achieve selected proportions of ramet emergence for three cohorts of *Arundo donax* ramets

	Proportion emerged	ACH	95% Fiducial limits
Cohort 1–ACH < 525			
0.01	44	−41	76
0.10	101	63	124
0.50	153	129	195
0.90	205	172	292
0.99	262	212	403
Cohort 2–ACH > 335 and <1210			
0.01	242	-22	377
0.10	504	368	581
0.50	745	687	807
0.90	986	905	1134
0.99	1249	1109	1525
Cohort 3–ACH > 1070 and <2500			
0.01	879	368	1099
0.10	1260	1005	1398
0.50	1609	1481	1780
0.90	1959	1787	2333
0.99	2341	2070	2986

For example, 0.9 or 90% of the ramets in cohort 1 should have emerged when 205 degree-days have been accumulated. ACH and 95% fiducial limits estimated using inverse prediction in the PROBIT PROCEDURE (SAS Institute Inc., 1999).

representation of processes involved in ramet emergence. The high R^2 values for linear regression of the model's predicted number of shoots and the actual number of shoots indicate that the relationships between these two variables are strong (Table 4). The effects of the significant intercept and slope for the 2001 data set offset each other, the intercept implies that the estimate is higher than the actual data, but the slope of less than one ($t = -8.69$, d.f. = 225, $P < 0.025$) compensates for this, yielding predictions which are quite good. In the 2002 data set the intercept was significantly different from zero, but the slope was not different from one ($t = 1.18$, d.f. = 131, $P > 0.025$) indicating that the model underestimated the actual data in 2002.

While it has been recognized that temperature is an important determinant of plant growth (Fitter and Hay, 2002; Thornley and Johnson, 1990), to our knowledge this is the first attempt to describe the emergence of *A. donax* ramets from rhizomes as a function of degree-days. Equations derived in this study fit the data well, and provide an underlying explanation for the temporally distinct patterns of emergence observed during the 2-year period of this study. The equations developed
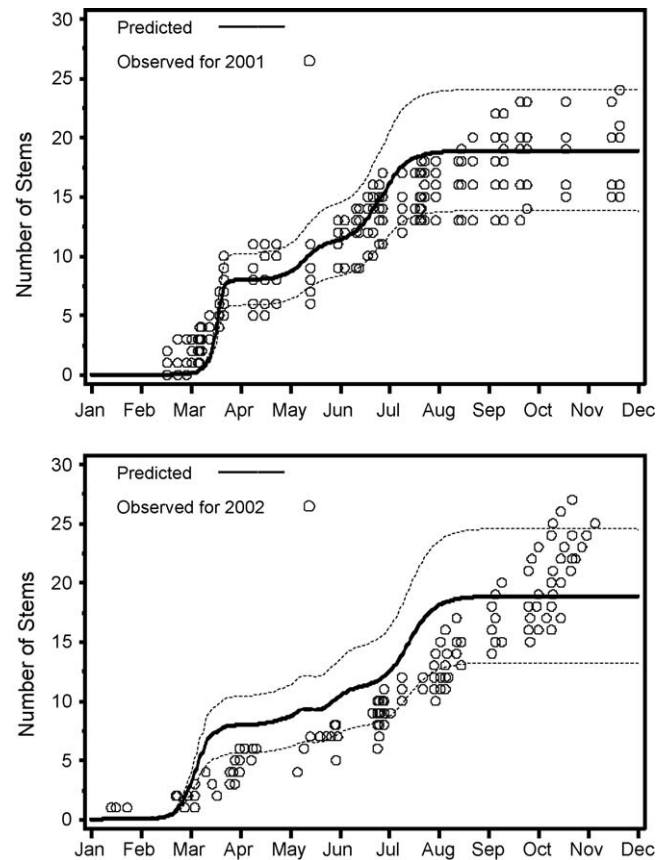

Fig. 6. Comparison of the predicted number of *Arundo donax* ramets (solid line) based on soil temperature from the 2001 and 2002 data sets and observed combined number of ramets for six individual plants in separate containers outdoors at Davis, California. The dashed lines represent predicted numbers using different numbers for cohort maximums. These values represent those equivalent to 95% confidence intervals for cohort maximum values from the 2001 data set.

for 1 year were capable of predicting emergence patterns in another year. This was likely due to the incorporation of both lower (7 °C) and upper (30 °C) thresholds for sprouting into the calculation of degree-days.

Previous studies that did not include an upper temperature threshold into the degree-day calculations were less successful at predicting growth stages across locations and years (Sanderson et al., 1994) Eliminating upper or lower thresholds may lead to estimates of degree-days that are either too low or too high (Zalom et al., 1983). Depending on temperature differences between locations, this deficiency may give the

Table 4
Linear regression equations relating the actual number of stems, the dependent variable, to the model estimated number of stems (slope), the independent variable for 2001 and 2002 data

Variable	DF	Parameter estimate	Standard error	*t*-Value	$Pr > |t|$	R^2	Year
Intercept	1, 227	1.61	0.28	5.68	<0.0001	0.88	2001
Slope		0.82	0.02	40.42	<0.0001		
Intercept	1, 133	−2.64	0.72	−3.67	0.0004	0.79	2002
Slope		1.06	0.05	22.28	<0.0001		

The *t*-test in this table tests the null hypothesis that the parameters are equal to zero.

appearance of differences between locations, which in reality may be artifacts of the methods of calculation. In the present study we estimated upper and lower thresholds based on empirical and published data, but more precise estimates of these parameters may be useful.

Acknowledgments

References

Allison, P.D., 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute, Inc., Cary, North Carolina, p. 288.

Bell, G., 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in Southern California. In: Brock, J.H., Wade, M., Pysek, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Blackhuys Publishers, Leiden, The Netherlands, pp. 103–113.

Boose, A.B., Holt, J.S., 1999. Environmental effects on asexual reproduction in *Arundo donax*. Weed Res. 39, 117–127.

Briske, D.D., Derner, J.D., 1998. Clonal biology of caespitose grasses. In: Cheplick, G.P. (Ed.), Population Biology of Grasses. Cambridge University Press, New York, NY, p. 399, pp. 106–135.

Cantor, A.B., 2003. SAS Survival Analysis Techniques for Medical Research, second ed. SAS Institute, Inc., Cary, North Carolina, p. 230.

Cook, C.D.K., 1990. Aquatic Plant Book. SPB Academic Publishing, The Hague, The Netherlands, p. 220.

Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M.O., 1985. Techniques in Bioproductivity and Photosynthesis, second ed. Pergamon Press, New York, p. 298.

Decruyenaere, J.G., Holt, J.S., 2001. Seasonality of clonal propagation in giant reed. Weed Sci. 49, 760–767.

DiTomaso, J.M., Healy, E.A., 2003. Aquatic and Riparian Weeds of the West, 3421. ANR Pub., University of California, p. 441.

Fitter, A.H., Hay, R.K.M., 2002. Environmental Physiology of Plants, third ed. Academic Press, San Diego, p. 367.

Gates, D.M., 1980. Biophysical Ecology. Springer-Verlag, New York, p. 611.

Goudriaan, J., Van Laar, H.H., 1994. Modelling Potential Crop Growth Processes: Textbook with Exercises. Kluwer Academic Publishers, Dordrecht, The Netherlands, p. 238.

Hunt, R., 1982. Plant Growth Curves: The Functional Approach to Plant Growth Analysis. University Park Press, Baltimore, p. 248.

Karssen, C.M., Hilhorst, H.W.M., 1992. Effect of chemical environment on seed germination. In: Fenner, M. (Ed.), Seeds, the Ecology of Regeneration in Plant Communities. CAB International, Wallingford, UK, pp. 327–348.

Lewandowski, I., Scurlock, J.M.O., Lindvall, E., Christou, M., 2003. The development and current status of perennial rhizomatous grasses as energy crops in the US and Europe. Biomed. Bioenerg. 25, 335–361.

Rathcke, B.R., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. Ann. Rev. Ecol. Syst. 16, 179–214.

Rossa, B., Tuffers, A.V., Naidoo, G., vonWillert, D.J., 1998. *Arundo donax* L. (Poaceae)—a C3 species with unusually high photosynthetic capacity. Bot. Acta 111, 216–221.

Sanderson, M.A., Karnezos, T.P., Matches, A.G., 1994. Morphological development of alfalfa as a function of growing degree-days. J. Prod. Agric. 7, 239–242.

SAS Institute Inc., 1999. SAS/STAT User's Guide, Version 8. SAS Institute Inc., Cary, North Carolina, p. 3884.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, third ed. W.H. Freeman and Company, New York, p. 887.

Spencer, D.F., Anderson, L.W.J., 1986. Photoperiod responses in monoecious and dioecious *Hydrilla verticillata*. Weed Sci. 34, 551–557.

Spencer, D.F., Ksander, G.G., 2001. Field evaluation of degree-day based equations for predicting sprouting of hydrilla (*Hydrilla verticillata*) turions and tubers. J. Freshwater Ecol. 16, 479–486.

Spencer, D.F., Ksander, G.G., Madsen, J.D., Owens, C.S., 2000. Emergence of vegetative propagules of *Potamogeton nodosus*, *Potamogeton pectinatus*, *Vallisneria american*, and *Hydrilla verticillata* based on accumulated degree-days. Aquat. Bot. 67, 237–249.

Thornley, J.H.M., Johnson, I.R., 1990. Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology. Clarendon Press, Oxford, p. 669.

Vitousek, P.M., 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57, 7–13.

Vitousek, P.M., Dantonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. N.Z. J. Ecol. 21, 1–16.

Wijte, A.H.B.M., Mizutani, T., Motamed, E.R., Merryfield, M.L., Miller, D.E., Alexander, D.E., 2005. Temperature and endogenous factors cause seasonal patterns in rooting by stem fragments of the invasive giant reed, *Arundo donax* (Poaceae). Int. J. Plant Sci. 166, 507–517.

Wilen, C.A., Holt, J.S., McCloskey, W.B., 1996. Predicting yellow nutsedge (*Cyperus esculentus*) emergence using degree-day models. Weed Sci. 44, 821–829.

Zalom, F.G., Goodell, P.B., Wilson, L.T., Barnett, W.W., Bentley, W.J., 1983. Degree-Days: The Calculation and Use of Heat Units in Pest Management. University of California, Division of Agriculture and Natural Resources Leaflet 21373, Berkeley, p. 10.